

Chapter 28 Knowledge of Social Relations

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The vervet monkeys had moved out of their sleeping trees to forage on the ground. While the adults fed, the juveniles played in a nearby bush. Macauley, the rambunctious son of a low-ranking female, wrestled Carlyle, the daughter of the highest-ranking female, to the ground. Carlyle screamed, chased Macauley away, and then went to forage next to her mother. Apparently the fight had been noticed by others, because a few minutes later Shelley, Carlyle's sister, approached Austen, Macauley's sister, and bit her on the tail.

REGARDLESS OF whether they are strepsirrhines, New World monkeys, Old World monkeys, or apes, nonhuman primates do not interact at random with the members of their own groups. Instead, as reviewed by Aureli and colleagues in chapter 23 of this volume, they interact in different ways with different individuals, in some cases forming close, enduring social bonds that may persist for months or even years (Seyfarth & Cheney 2012 for review). These differentiated relationships constitute the animals' social environment. What do they know about it? Do they recognize the relationships that exist among other individuals? In this chapter we examine primates' social knowledge and consider what it may reveal about the evolution of cognition in human and nonhuman species.

Research on primate social cognition is of general interest for several reasons. First, it addresses central issues in the study of animal learning. A vervet monkey (*Chlorocebus pygerythrus*) is not born knowing about the relation between Shelley and Carlyle; instead, she must learn about other animals' relationships from what she sees and hears

around her. This knowledge, it turns out, can be surprisingly complex, not least because it may involve as many as 100 different individuals. Can we explain it using the same principles of classical and operant conditioning that guide our understanding of learning in other species?

Second, data on primate social cognition are central to the social intelligence hypothesis (Jolly 1966; Humphrey 1976), which begins with the observation that primates have larger brains for their body size than other vertebrates (Martin 1990). This difference has arisen, the hypothesis argues, because primate groups are larger and their social relationships are more complex than those in other taxa (e.g., Dunbar 2000, 2003). Their large brains have evolved both to manage their own relationships and to recognize and "track" the relations among others. But are nonhuman primate relationships really different from those in other species? Is their social knowledge more extensive?

Third, if sophisticated social cognition is a pervasive feature of life in primate groups, how did this trait evolve? What, precisely, is the link between social intelligence and increased survival and reproduction?

Over the past 20 years scientists have made considerable progress in addressing these questions. Some are now firmly settled; answers to others are only beginning to emerge.

Brain Specializations for Social Stimuli

Regardless of their brain size or the complexity of their social behavior, all animals respond selectively to stimuli produced by members of their own species. Solitary frogs

respond more strongly to their own species' calls than to calls of another species (Gerhardt & Bee 2006); monogamous birds respond more strongly to their own species' song (Benney & Braaten 2000). Primates are no different. Rhesus macaques (*Macaca mulatta*), for example, have "face cells" in the temporal cortex that respond at least twice as vigorously to faces or components of faces (like eyes or mouths) than to other complex visual stimuli (Tsao 2003, 2006). Face cells are surprisingly specialized. Those in the inferior temporal cortex (IT) seem most important for processing facial identity, whereas those in the superior temporal sulcus (STS) seem most important for processing facial expressions. IT and STS are extensively interconnected and probably share face-specific information (see Ghazanfar & Santos 2004 for review). Face cells in STS respond not only to facial expressions but also to the direction of an individual's head orientation and gaze. Their response is greatest when head orientation and gaze direction are congruent, and less strong when they are incongruent (Perrett et al. 1992; Emery & Perrett 2000; Jellema et al. 2000; Eifuku et al. 2004). The STS of rhesus macaques also includes neurons that fire when the monkey observes an individual walking, turning his head, bending, or extending his arm (Perrett et al. 1990). Particularly intriguing are "mirror neurons" in the inferior parietal lobule that show elevated activity both when the subject monkey executes a specific grasping action and when the monkey observes a human or other monkey executing a more or less similar grasp (Rizzolatti & Craighero 2004).

Rhesus macaques also process their own species' vocalizations in ways that are measurably different from the way they process other auditory stimuli. Like humans, they have brain areas that appear to be specialized for the recognition of different speakers (Belin & Zattore 2003; Petkov et al. 2008). Rhesus and Japanese macaques (*Macaca fuscata*) also display a left-brain, right-ear advantage when processing their own species' vocalizations but not when processing other sounds (Petersen et al. 1978; Hefner & Hefner 1984; Weiss et al. 2002; Poremba et al. 2004).

Specialized brain mechanisms for dealing with social stimuli do not, by themselves, confirm the social intelligence hypothesis—particularly because we find such specializations in many species despite wide variation in brain size and apparent social complexity. But the special responsiveness of the primate brain to conspecific voices, faces, gaze direction, and actions are just what we would expect if natural selection had acted to favor individuals skilled in solving social problems. Particularly intriguing is evidence that the STS and mirror neurons are also highly sensitive to intentional, goal-directed behavior, which indicates that they may help animals assess other individuals' intentions.

Recognition of Stable, Long-Term Relations in New and Old World Monkeys

Some features of primate social relationships are stable and predictable over long periods of time. For example, the adult females in many New and Old World monkey species form stable, long-term dominance hierarchies in which individual members of the same matriline—mothers, daughters, and sisters—maintain close relationships characterized by high rates of grooming, solicitations for grooming, mutual tolerance at feeding sites, and aggressive coalitions. Such bonds may last for 5, 10, or even 20 years (baboons, genus *Papio*, Silk et al. 2006a, 2006b; Cheney & Seyfarth 2007; rhesus macaques, Sade 1972; Japanese macaques, Kawai 1958; Koyama 1967; wedge-capped capuchins, *Cebus olivaceus*, O'Brien & Robinson 1993; white-faced capuchins, *Cebus capucinus*, Perry et al. 2008). Members of the same matriline occupy adjacent dominance ranks, and matriline rank above one another in a "hierarchy of families." Both within and between families, ranks are linear and transitive (A dominates B, B dominates C, C dominates D, and so on). Typically, ranks remain stable for years at a time. Under these conditions, where highly predictable relations are so clear to a human observer, it is reasonable to ask whether the animals themselves recognize the kin and rank relations that exist among their companions. Evidence that they do so comes from both observational and experimental studies.

Recognition of Other Animals' Matrilineal Kin Relations

In many species, natural patterns of aggression and reconciliation suggest that animals have some knowledge of the close relations that exist among matrilineal kin. (Note that when we refer to monkeys' ability to recognize other individuals' kin, we mean only that monkeys recognize the close bonds that exist among kin. There is as yet no evidence that they distinguish the close bond that exists between two sisters, for instance, from the bond that exists between a mother and her adult daughter). Often, for example, an individual that has just been involved in an aggressive interaction with another will redirect aggression by attacking a third, previously uninvolved animal. Judge (1982, 1991) was the first to note that redirected aggression does not occur at random. He found that rhesus macaques do not simply threaten the nearest lower-ranking individual; instead, they target a close matrilineal relative of their opponent. Similar kin-biased redirected aggression occurs in Japanese macaques (Aureli et al. 1992) and vervet monkeys (Cheney & Seyfarth 1986, 1989). In a study of captive stump-tailed macaques (*Macaca arctoides*), Call et al. (2002) found that following aggression recipients di-

rected an increased amount of sociosexual behavior toward all others in their group except their opponent's matrilineal kin, thus providing indirect evidence for their recognition of others' close relations.

When two white-faced capuchin monkeys are involved in an aggressive interaction, one or both of the combatants may attempt to recruit an ally. The monkeys' pattern of recruitment attempts also demonstrates their knowledge of other animals' close relations. Over a two-year period, Perry et al. (2004, 2008) found that individuals preferentially solicited allies who (1) ranked higher than their opponents and (2) had a social relationship with the solicitor that was closer (as measured by the ratio of past affiliative to aggressive interactions) than their relationship with the opponent. Although preferential solicitation of higher-ranking individuals could have occurred because individuals simply followed one of two simple rules ("Solicit an animal that ranks higher than yourself" or "Solicit the highest-ranking individual available"), the preferential solicitation of more closely bonded individuals could be explained only by assuming that solicitors were somehow comparing the bond between the ally and themselves with the bond between the ally and their opponent (Perry et al. 2004, 2008).

Supplementing these observational studies, field audio playback experiments provide independent evidence that individual monkeys recognize other animals' kin relations. In one study, a recording of a juvenile vervet monkey's distress scream was played to a group of three females, one of whom was the juvenile's mother. As expected, the mother looked toward the loudspeaker for longer durations of time than did the two control females. In addition, however, the control females responded by looking toward the mother, often reacting before the mother herself had responded. They behaved as if they associated the call with a specific juvenile, and that juvenile with a specific adult female (Cheney & Seyfarth 1980).

In another study, two unrelated adult female chacma baboons (*Papio ursinus*) served as subjects. On three different occasions, a pair of subjects heard a sequence of calls consisting of two other individuals' threat-grunts and screams. The calls were designed to mimic a common aggressive interaction in which a higher-ranking baboon gives threat-grunts to a lower-ranking animal, and the lower-ranking animal screams. In the first control condition, both of the apparent combatants were unrelated to the subjects. In the second, one of the combatants was a close relative of the dominant subject, while the other was unrelated to either female. In the third test condition, one of the combatants was a close relative of the dominant subject and the other was a close relative of the subordinate subject. When females heard a sequence that mimicked a dispute between

two individuals unrelated to them, they showed little or no reaction. When they heard a sequence that involved a relative of the dominant subject, the subordinate looked at the dominant but the dominant rarely looked at the subordinate. But when they heard a sequence that involved their relatives, both females looked at each other. Equally striking was that the dominant subject was more likely to seek out the subordinate subject and supplant her in the half-hour that followed these trials than in the half-hour that followed the two control sequences. Subjects behaved as if they recognized that a conflict between their families had occurred and had temporarily disrupted their relationship (Cheney & Seyfarth 1999).

Many primates "reconcile" with an opponent by touching, hugging, or behaving in a friendly way towards the opponent after aggression (Cords 1992; de Waal 1996; chapter 23, this volume). In baboons, reconciliation often takes the form of a grunt given by the aggressor to her former victim (Silk et al. 1996). Audio playback experiments confirm that grunts given by the aggressor after a fight change the victim's behavior, thus increasing the likelihood that the victim will interact in a friendly or tolerant way toward the aggressor—hence the description of this behavior as "reconciliation" (Cheney et al. 1995b; Cheney & Seyfarth 1997). Further experiments have shown that the grunts of a close relative of the aggressor can also function as a proxy to reconcile opponents. Specifically, victims of aggression are more likely to tolerate their opponent's proximity in the hour after the dispute if they have heard the grunt of their opponent's relative than if they have heard the grunt of a more dominant individual belonging to a different matriline (Wittig et al. 2007a). Such kin-mediated reconciliation succeeds only when the victim recognizes the relationships that exist among other group members (see also Das 2000; Judge & Mullen 2005). Conversely, if the victim hears the threat-grunt of her opponent's relative shortly after aggression, she is more likely to avoid her opponent and other members of her opponent's matriline (Cheney & Seyfarth 2007; Wittig et al. 2007b).

The experiments on baboons' responses to kin-mediated reconciliation and vocal alliances support the view that baboons recognize other females' matrilineal kinship relations. This is not to say, however, that baboons treat all the members of a matriline as equivalent. Although they recognize that close kin can serve as proxies for each other, they nonetheless distinguish among the different members of a matriline. Hearing a "reconciliatory" grunt from an opponent's relative changes females' behavior toward the opponent and that relative, but not toward other members of the opponent's matriline (Cheney & Seyfarth 2007; see Rendall et al. 1996 for experiments demonstrating the recognition

of individuals and of close relations among matrilineal kin in rhesus macaques).

What learning mechanisms underlie this behavior? Considered in isolation, the recognition of other animals' close kin relations would seem to require no special skills beyond those well documented in laboratory studies of learning. All a young primate needs to do is observe and memorize who interacts with whom, and note differences in the quality of their interactions. The recognition of matrilineal kin, however, does not occur in isolation: matrilineal kin relations are embedded in a network of short- and long-term bonds that vary among individuals according to age, rank, reproductive state, and many other variables. Whether social knowledge under natural conditions, in all its simultaneous manifestations, can be explained by simple theories of association remains an open issue. We discuss some competing hypotheses below.

Recognition of Other Animals' Dominance Ranks

Like the bonds among matrilineal kin, linear, transitive dominance relations are a pervasive feature of behavior in many primate groups (chapter 9, this volume). A linear rank hierarchy might emerge because a female simply takes note of who is dominant and subordinate to herself—an egocentric view of the world, but one that nonetheless would result in a linear, transitive rank order. Alternatively, the female might also distinguish among the relative ranks of others. If rank were determined by a physical attribute like size, recognizing other individuals' ranks would be easy. Among most female monkeys, however, there is no relation between rank and size, condition, age, or any other obvious feature. As a result, the problem is considerably more challenging.

There are hints from their behavior that monkeys do recognize other individuals' relative dominance ranks. In a meta-analysis of 14 different species, including New and Old World monkeys, Schino (2001) found consistent evidence that high-ranking females received more grooming and were groomed by more different individuals than lower-ranking females. These data suggest a general preference for grooming high-ranking individuals, but they fall short of showing that each animal recognizes the relative ranks of others. In subsequent papers, Schino used a within-subject regression analysis to test the hypothesis that each individual distributed grooming among others in direct relation to their relative rank. He found a significant rank effect in Japanese macaques (Schino et al. 2007) but not in tufted capuchins (*Cebus apella*, Schino et al. 2009).

In vervet monkeys, females solicit grooming from others by presenting a part of their body to them. The solicited individual may or may not accept the invitation. In general,

females are most likely to accept the solicitations of the highest-ranking female, second most likely to accept those of the second-ranking female, third most likely to accept those of the third-ranking female, and so on (Seyfarth 1980).

Knowledge of other individuals' rank relations also appears in patterns of recruitment and coalition formation. When two female vervets, macaques, or baboons are involved in an aggressive interaction and a third female, higher-ranking than both, joins them to form a coalition, the third female almost always supports the higher-ranking individual (vervets, Seyfarth 1980; Cheney 1983; rhesus macaques, de Waal 1991; Japanese macaques, Chapais 2001; but for contrary data on chimpanzees [*Pan troglodytes*], gorillas [*Gorilla gorilla*], and white-faced capuchins, see de Waal & van Hooff 1981; Watts 1991; and Perry 2003).

Similarly, when recruiting alliance partners, monkeys often appear to be assessing not only their own rank relative to a potential ally but also the rank relation between the prospective ally and their opponent. As already noted, white-faced capuchin monkeys consistently recruit allies who outrank their opponents, but this pattern of recruitment could result from individuals following the simple rule "Solicit an ally who ranks higher than yourself" or "Solicit the highest-ranking animal available." By contrast, in Silk's (1993, 1999) study of captive male bonnet macaques (*Macaca radiata*), the pattern of solicitation could only be explained by assuming that males tried preferentially to recruit allies that outranked both themselves and their opponents. Furthermore, the males' choice of alliance partner varied depending on their opponent's rank. If a male was involved in a fight with the seventh-ranking male, he would attempt to solicit the aid of, say, the fifth-ranking male. But if his opponent was the twelfth-ranking male, he would attempt to recruit the ninth-ranking one. If the male dominance hierarchy had remained stable, memorizing each male's rank might not have been a difficult task, but each month roughly half of the 16 males changed rank. The males' behavior suggests that they carefully monitored all aggressive interactions and constantly updated their list.

These observations are supported by field experiments. In one study, for example, chacma baboons heard a sequence of vocalizations mimicking an interaction that violated the female dominance hierarchy. The sequence consisted of a series of grunts originally recorded from a lower-ranking female (say, the fifth-ranking female) combined with a series of fear barks originally recorded from a higher-ranking female (say, the third-ranking female). This sequence violated the female dominance hierarchy because, whereas baboons routinely grunt both to lower- and higher-ranking individuals, they give fear-barks only to individuals that rank above them. In control trials, subjects heard the same

anomalous sequence of calls, but with the grunts of a third female that normally outranked both of the other individuals (say, the second-ranking female). This sequence was consistent with the female dominance hierarchy because the third-ranking female could be giving fear-barks to the second-ranking female rather than the fifth-ranking one. Supporting the view that baboons recognize other individuals' dominance ranks, subjects looked in the direction of the loudspeaker for significantly longer durations when they heard the sequence that violated the dominance hierarchy (Cheney et al. 1995a).

The recognition of other individuals' dominance ranks has also been documented among adult male chacma baboons, whose aggressive contests often involve loud "wahoo" calls given by two or more males as they race through the group, climb trees, and leap from branch to branch (Kitchen et al. 2003; Fischer et al. 2004). In this experiment, individual males heard wahoo sequences that mimicked a contest between either adjacently ranked or disparately ranked males. To control for the fact that wahoo contests involving adjacently ranked males are more common than those involving males of disparate ranks, only the calls of adjacently and disparately ranked males who had interacted at the same rate during the past six months were used as stimuli. High-ranking male subjects responded significantly more strongly to the audio playback of a wahoo contest between males of disparate ranks than to the playback of a contest between males of adjacent ranks (Kitchen et al. 2005). This result might have arisen because adjacently ranked males compete with one another in many different contexts, whereas males of disparate ranks tend to compete only when the resource at stake is highly valued: meat, a sexually receptive female, or an infant vulnerable to infanticide. Whatever the explanation, results suggested that males could assess the rank distance between any two males (Kitchen et al. 2005). The result is particularly striking because, like the ranks of male bonnet macaques described earlier, the ranks of male baboons change often.

Like the recognition of other animals' kin relations, the recognition of other animals' rank relations may have been favored by natural selection because it allows individuals to groom, recruit allies, and form coalitions most effectively. Some scientists have argued that rank recognition should be most well developed in species where dominance hierarchies are most pronounced. Thierry (2008) and Schino and Aureli (2008) review evidence to support this view. For example, the ability to recognize other individuals' ranks implies the ability to make transitive inferences: to recognize that, if A is greater than B and B is greater than C, then A must be greater than C. In an experimental test of transitive inference, Maclean et al. (2008) found that ring-tailed

lemurs (*Lemur catta*), which live in large groups with linear dominance hierarchies, performed better than mongoose lemurs (*Eulemur mongoz*), which live in small, monogamous pairs. After extensive training, however, the two species performed equally well.

The ability to engage in transitive inference seems to have evolved independently in many species with linear dominance hierarchies. When forming a coalition, spotted hyenas (*Crocuta crocuta*) consistently join the higher-ranking of two competitors, regardless of which one is winning at the time (Engh et al. 2005). Pinyon jays (*Gymnorhinus cyanocephalus*)—often called "avian baboons"—live in stable flocks of 50 to 500 individuals, each containing individuals that are linked by kinship and arranged in a linear dominance hierarchy. Elegant experiments by Paz-y-Miño et al. (2004) have shown that jays use transitive inference to calculate their own dominance status relative to that of a stranger they have observed interacting with their group mates. Grosenick et al. (2007) performed a similar experiment on fish (*Astatotilapia burtoni*), with similar results.

Regardless of how it evolved, the recognition of other individuals' rank relations, like the recognition of other animals' matrilineal kin relations, requires by itself no special skills in learning and intelligence beyond those well documented in laboratory studies of classical conditioning. Individuals simply need to observe the behavior of others, remember what has happened in the past, and update their knowledge as new information becomes available. In nature, however, recognition of other animals' ranks does not occur on its own; it must necessarily be integrated into a complex matrix of other social relations. We are only beginning to understand how this is achieved.

Integrating Knowledge of Kin and Rank Relations

Having found that chacma baboons recognize the close bonds among matrilineal kin and individual dominance ranks, Bergman et al. (2003) tested whether individuals integrated their knowledge of other individuals' kinship and rank to recognize that the female dominance hierarchy is in fact composed of a hierarchy of families (that is, subgroups of closely bonded females). As background, recall that rank relations among adult female baboons are generally very stable over time, with few rank reversals occurring either within or between families. When rare reversals do occur, their consequences differ significantly depending on who is involved. If, for example, the third-ranking female in matriline B (B_3) rises in rank above her second-ranking sister (B_2), the reversal affects only the two individuals involved; the family's rank relative to other families remains unchanged. However, a rare rank reversal between two females from

different matriline (for example, C_1 rising in rank above B_3) is potentially much more momentous because it can affect entire families, with all the members of one matriline (in this case, the C matriline) rising in rank above all the members of another.

Bergman et al. (2003) played sequences of calls mimicking rank reversals to subjects in paired trials. In one set of trials, the subjects heard an apparent rank reversal involving two members of the same matriline: for example, female B_3 giving threat-grunts while female B_2 screamed. In the other set, the same subjects heard an apparent rank reversal involving the members of two different matrilines: for example, female C_1 giving threat-grunts while female B_3 screamed. As a control, the subjects also heard a fight sequence that was consistent with the female dominance hierarchy. To control for the rank distance separating the subjects and the individuals whose calls were being played, each subject heard a rank reversal (either within- or between-family) that involved the matriline one step above her own (cf. Penn et al. 2008). Within this constraint, the rank distance separating apparent opponents within and between families was systematically varied.

As before, listeners responded with apparent surprise to sequences of calls that appear to violate the existing dominance hierarchy. Moreover, between-family rank reversals elicited a consistently stronger response than did within-family rank reversals (Bergman et al. 2003). The subjects acted as if they classified individuals simultaneously according to both kinship and rank. The classification of individuals simultaneously according to two different criteria has also been documented in Japanese macaques (Schino et al. 2006).

Recognition of More Transient Social Relations

Bonds among matrilineal kin and a linear, transitive female dominance hierarchy are components of monkey social structure that typically remain stable for many years. It is perhaps not surprising, therefore, that primate social cognition has been best documented in these two domains. There is growing evidence, however, that primates also recognize and monitor more transient social bonds.

Hamadryas baboons (*Papio hamadryas*) in Ethiopia are organized into one-male units, each containing a fully adult male and two to nine adult females (Kummer 1968; Stambach 1987; chapter 5, this volume). One-male units frequently come into contact with single, unattached males who may attempt to challenge the unit leader in an attempt to take over his females. In the first experimental test of individuals' ability to recognize other animals' relations, Bachmann and Kummer (1980) found that the willingness of a male to challenge a unit leader depended not on the

challenger's dominance rank relative to that of the leader, but on the challenger's perception of the strength of the bond between the leader and his females. Noting that social bonds between adult males and females can change often, Bachmann and Kummer suggested that challengers continually monitor one-male units to assess whether the bonds between a male and his females have weakened.

Just this kind of monitoring seems to occur in multi-male groups of baboons, where males form sexual consortships with an adult female during the week when she is most likely to ovulate (chapter 18, this volume). Sexual consortships constitute a form of mate guarding, and typically involve the highest-ranking male. When a consortship has been formed, lower-ranking males can nonetheless gain mating opportunities by taking advantage of temporary separations between a female and her consort to mate "sneakily" (chapter 18, this volume). To test whether subordinate males monitor sexual consortships for such opportunities in chacma baboons, Crockford et al. (2007) used a two-speaker playback experiment to simulate a temporary separation between the consort pair. One speaker played the consort male's grunt to signal his location. The other speaker, located approximately 40 meters away, played the female's copulation call to signal that she was mating with another male and that further mating opportunities might be available. The subordinate males responded immediately to the apparent separation between the female and her consort by approaching the speaker playing the female's call. By contrast, when the same playback was repeated a few hours after the consortship had ended, the subordinate males showed no interest. Apparently, they already knew that the consortship had ended, and the information was therefore redundant. Thus, males appear to monitor the status of these transient consort relationships very closely, even though they typically last for only a few days (see Smuts 1985 for similar data on animals' recognition of the "friendships" between males and lactating females in olive baboons, *Papio anubis*).

The Recognition of Social Relationships in Fission-Fusion Societies

The fission-fusion societies found in many animals, including spider monkeys (*Ateles* spp., chapter 3, this volume) and chimpanzees (chapter 6, this volume), may present animals with challenges and selective pressures not found in species where all individuals in a group travel, interact, and sleep as a unit (Aureli et al. 2008). Thus far, the only data on social knowledge in a primate with a fission-fusion society come from studies of chimpanzees, so they are the focus of this

section. Recognizing other animals' relations in chimpanzee society presents a challenge, for several reasons.

First, whereas the close social bonds found in monkeys involve a relatively small number of behaviors like grooming, coalitions, and tolerance at food sources, the long-term bonds formed by chimpanzees include behaviors as diverse as mate guarding (Watts 1998), coalitions in male-male competition (Nishida & Hosaka 1996), cooperative defense of territories (Mitani et al. 2010), grooming, and meat sharing (Wittig & Boesch 2003; Mitani 2006, 2009). To monitor and distinguish the different relationships within its group, therefore, a chimpanzee must keep track of many more behaviors.

Second, as in many species of New and Old World monkeys (see above), but perhaps to an even greater extent, the interactions that characterize close bonds in chimpanzees are often widely separated in time. Among male chimpanzees at Ngogo, for example, the pairs who groom most often also have the highest rates of coalition formation and participation in border patrols, yet these behaviors do not necessarily occur together in time (Mitani 2006, 2009). Days may pass between a grooming bout and the formation of a coalition or a border patrol. Further complicating matters, there may be striking short-term "imbalances" in cooperative behavior within a close relationship. Pairs with the strongest grooming relations and the strongest bonds overall may have grooming that is highly imbalanced within a bout (one partner does most of the grooming) but highly equitable over longer periods of time (Gomes et al. 2009; Mitani 2009). The most closely bonded chimpanzees, like the most closely bonded baboons, seem "tolerant of temporary imbalances" in their relationship (Silk et al. 2010a, p. 1743; Seyfarth & Cheney 2012). As a result, an observer attempting to distinguish bonds of different strength cannot do this by observing a single grooming session.

Third, the correlations among behaviors that distinguish long-term bonds in chimpanzees can be complex. In the Tai forest, for example, male-male, male-female, and female-female dyads with the strongest, most enduring bonds as measured by meat sharing and the rate of coalition formation also had the highest rates of grooming, but not the highest rates of spatial association. Rates of meat sharing and coalition formation, but not rates of grooming, predicted the rate at which dyads reconciled following aggression (Wittig & Boesch 2005; Wittig 2010). An observer attempting to distinguish closely bonded pairs from others must therefore take note of and remember many different behaviors.

Despite the complexity of their behavior and society, chimpanzees not only maintain close, long-term bonds with specific partners (Mitani 2009; Wittig 2010; chapter 6, this volume), but also recognize and distinguish the dif-

ferent relationships that exist among others (see Seyfarth & Cheney 2012 for review). For example, sometimes after an aggressive interaction between two individuals a previously uninvolved bystander will direct friendly behavior toward the victim. In one study, the probability that a bystander would engage in such behavior depended primarily on the strength of the bond between the bystander and the victim: the stronger their bond, the more likely that such "consolation" would occur (Kutsukake & Castles 2004). In another study, however, the bystander was most likely to direct friendly behavior toward the victim if the bystander had a strong bond with the aggressor and a weak bond with the victim (Wittig 2010). Moreover, if the bystander had a strong bond with the aggressor, this increased the likelihood that the aggressor and victim would tolerate each other's proximity in the near future; but if the bystander had a weak bond with the aggressor, this effect disappeared (Wittig & Boesch 2010). Victims acted as if they recognized the close bond (or lack of it) between the bystander and the aggressor. As a result, they treated the bystander's friendly behavior as "reconciliation by proxy" only if the bystander was a close associate of the aggressor.

Chimpanzees often scream when involved in aggressive disputes. Slocombe and Zuberbühler (2005) found that victims produce acoustically different screams according to the severity of aggression they are receiving. In playback experiments, listeners responded differently to the different scream types (Slocombe et al. 2009). In cases of severe aggression, victims' screams sometimes seemed to exaggerate the severity of the attack, but victims only gave exaggerated screams if their foraging party included at least one listener whose dominance rank was equal to or higher than that of their aggressor (Slocombe & Zuberbühler 2007). Victims seemed to alter their screams depending upon the relationships between their opponent and their potential allies.

The Recognition of Intentions and Motives

Although it now seems clear that many animals recognize other group members' relationships and dominance ranks (cf. Henzi & Barrett 2007), we still know little about whether they attribute to these relationships a particular set of emotions and motives, as humans do. In the more than 30 years since Premack and Woodruff (1978) posed the question "Does the ape have a theory of mind?," much progress has been made in the study of mental state attribution in animals. Many questions, however, remain unresolved (chapters 30 and 32, this volume).

Several lines of evidence suggest that primates routinely attribute simple mental states, like intentions and motives,

to others. In the wild, this ability is particularly evident in their response to vocalizations, when individuals must make inferences about the intended recipient of another animal's calls. This is not surprising: primate groups are noisy, tumultuous societies, and an individual could never manage her social interactions if she assumed that every vocalization was directed at her. Inferences about the directness of vocalizations are probably often mediated by the direction of the caller's gaze. Even in the absence of visual signals, however, monkeys seem to make inferences about the intended recipient of a call based on their knowledge of a signaler's identity and the nature of recent interactions.

Recall, for example, that a female baboon responded strongly when she was played a recording of her aggressor's grunt within minutes after being threatened, but showed little response if she heard the grunt of another dominant female unrelated to her aggressor. In other words, the female responded as if the aggressor's grunt was directed *to her*, but the other individual's grunt was directed to someone else. Moreover, the female's responses to the aggressor's grunt (she approached the aggressor and/or tolerated the aggressor's approach) indicated that she treated the call as a "reconciliatory" signal of benign intent. In other words, she attributed specific motives to the aggressor.

These results were replicated in one test where female baboons heard the "reconciliatory" grunt of their aggressor's kin and likewise treated it as a reconciliatory signal (see above). They were further replicated in a second test where subjects heard an aggressive threat-grunt from an individual after they had either exchanged aggression or groomed with that same individual (Engh et al. 2006c). Subjects who heard a female's threat-grunt shortly after grooming with her ignored the call—they acted as if they assumed that the female was threatening another individual. By contrast, the same subjects responded strongly when they heard the same call after receiving aggression; they acted as if the call was directed *at them*.

In sum, while nonhuman primates may lack a full-blown "theory of mind" like that found in young children (chapters 30 and 32, this volume), they do appear to attribute simple emotions and motivational states to others. Their knowledge of social relationships may well be closely linked to these attributions (de Waal 2008; Schino & Aureli 2009; Seyfarth & Cheney 2012).

Testing the Social Intelligence Hypothesis

Can primate social knowledge be explained by traditional theories of learning? Are the societies of nonhuman primates more complex than those of other species? Is their

social intelligence more impressive? Finally, regardless of whether primate social intelligence exceeds that found in other species, what role has social intelligence played in primate evolution? How does it translate into improved reproductive success? These questions, by no means resolved, are central to tests of the social intelligence hypothesis. We consider them in turn.

Are Traditional Theories of Learning Sufficient?

Can a few simple rules explain the complexity of primates' social knowledge? Some learning psychologists believe that they can, and have argued that monkeys' apparent recognition of other individuals' kin (to cite one example) is simply an impressive form of associative learning and conditioning.

It is well known that laboratory animals like rats and pigeons can be taught to group even very different looking stimuli together if they are all associated with the same reward or outcome. In one series of tests, Schusterman and Kastak (1993, 1998) taught Rio, a California sea lion (*Zalophus californianus*), to group arbitrary symbols into "equivalence classes." Each group consisted of three cards depicting a symbol: for example, a pipe (A_1), a fish (A_2), and a star (A_3). The experimenters arranged the symbols into equivalence classes by displaying one group of cards (say, A_1 , A_2 , and A_3) next to each other on one side of Rio's enclosure and another group of cards (say, B_1 , B_2 , and B_3) next to each other on the other side. After a few days' exposure, Rio was presented with one card from the A class and one card from the B class (A_1 and B_1). As soon as she prodded one of the cards with her nose, she was rewarded with food. Assuming that Rio chose A_1 rather than B_1 , she then received repeated presentations of the same cards, with A_1 always rewarded and B_1 not rewarded, until she achieved a 90% success rate. Then Rio was tested, first with symbols A_2 and B_2 (transfer test 1) and next with symbols A_3 and B_3 (transfer test 2), to determine whether she had learned to treat all A stimuli as equivalent to each other and all B stimuli as equivalent to each other, at least insofar as they followed the rule "If A_1 is greater than B_1 , then A_n is greater than B_n ." Rio performed correctly on 28 of 30 transfer tests.

Schusterman and Kastak argue that these relatively simple equivalence judgments constitute a general learning process that underlies much of the social behavior of animals, including the recognition of social relationships by monkeys and apes (for similar arguments see Heyes 1994; Wasserman and Astley 1994; Thompson 1995). This argument has much validity. Indeed, it is hard to imagine how a monkey could learn that two other individuals were members of the same matriline except by grouping them together

by virtue of their high rates of association. At the same time, however, the “equivalence classes” found in nonhuman primate groups exhibit complexities not present in laboratory experiments.

First, consider the magnitude of the problem. The sea lion Rio was confronted with a total of 180 dyadic comparisons. This is roughly equivalent to the number of different dyads that confront a monkey in a group of 18 individuals. But the number of possible dyads increases rapidly as group size increases. Baboons, for example, often live in groups of 80 individuals, which contain 3,160 different dyads and 82,160 different triads. As a result, individuals face problems in learning and memory that are not just quantitatively but also qualitatively different from those presented in a typical laboratory experiment. This is important, because it is large numbers that may force primates to develop rules to classify their group mates.

Second, in primate groups no single metric specifies the associations between individuals. It is, of course, a truism that animals can learn which other individuals share a close social relationship by watching them interact. But no single behavioral measure is either necessary or sufficient to recognize such associations. Aggression often occurs at the same rate within and between families, and different family members may groom and associate with each other at widely different rates (e.g., Silk et al. 2010a). Spatial proximity is not a defining characteristic of close bonds among female baboons, but it is invariably present in the bond between a male and his sexual consort (Crockford et al. 2007). In sum, there is no threshold or simple defining criterion for a “close” social bond among primates. By contrast, in Schusterman and Kastak’s experiments the spatial and temporal juxtaposition of stimuli provided an easy, one-dimensional method for the formation of equivalence classes.

Third, class members in monkey groups are sometimes mutually substitutable, and sometimes not. Consider, for example, the early experiment on vervet monkeys, in which females who heard a juvenile’s screams then looked toward the juvenile’s mother. Schusterman and Kastak (1998) argue that this occurs because the scream, the juvenile, and the juvenile’s mother form a three-member equivalence class in the females’ minds in which any one of the stimuli can be substituted for another. But in fact the call, the juvenile, and the mother are not interchangeable. A female who has a close bond with the juvenile’s mother, for example, may interact very little with the juvenile himself. The call is linked primarily to the juvenile, and only secondarily to the mother. Indeed, audio playback experiments on rhesus macaques have shown that, although monkeys do group calls given by members of the same matriline into the same category, they also distinguish among the calls given by different individu-

als within that matriline (Rendall et al. 1996; see also the “reconciliatory” grunt experiments discussed above).

Fourth, some social relationships are transitive, but others are not. In baboon society, if an infant and a juvenile both associate at high rates with the same adult female, it is usually correct to infer that the two are siblings and will also associate at high rates. Similarly, if a lactating female associates at a high rate with a particular adult male friend, it is probably correct to assume that the male is also closely allied to the female’s infant. It would be incorrect, though, to make the same assumption about the juvenile, because males seldom interact at high rates with their friends’ older offspring. In fact, the juvenile is more likely to associate with a different male—the male who was his mother’s friend when he was an infant.

Further complicating matters, individuals can belong to many different classes simultaneously. An adult female baboon, for instance, belongs to a matrilineal kin group, associates with one or more adult males, holds a particular dominance rank, and may be weakly or strongly linked to other females outside her matriline. Here again, the natural situation is considerably more complex than the situation in most laboratory settings.

Finally, some types of class membership change often. While the rank and kin relations among female monkeys are often relatively stable, other social relationships change often and unpredictably. Yet individuals are able to monitor these changes and make the appropriate adjustments.

In sum, there is no doubt that associative processes and contingency-based learning provide powerful ways to assess the relationships that exist among others. However, in order to conclude that all primate social knowledge results from simple learning mechanisms, we need proof that these mechanisms can account for behavior as complex as that which occurs in free-ranging primate groups. Suppose that the sea lion Rio were trained with an array of 80 items (the approximate size of a baboon group), each of which associated at varying rates with all 79 other items, but at high rates with a subset of the items. Item A, for example, might associate at a high rate with items B, C, D, and E. Item B might also associate with these items, but at a different rate than A. Item B would also associate with some items with which A rarely associated. To complicate matters further, there would also be brief, transient associations of varying duration between pairs of items that cut across the links formed between items that associated at a high rate. Under these circumstances, could Rio learn to group the items that associate at high rates into “kin” classes while simultaneously keeping track of the transient pairings that cut across classes? Perhaps Rio would rise to the occasion; perhaps not.

Laboratory experiments designed to explain complex behavior using the simplest explanation possible have limited external validity if they leave out the very complexity they hope to explain, or depend on extensive training and reinforcement. Primates, after all, derive no immediate and predictable rewards from their knowledge of other individuals' social relationships—unless we assume that they find social spectatorship inherently rewarding. But if we accept this view and assume that primates are motivated by the inherent value of acquiring knowledge about others, our concepts of reward and reinforcement must become considerably broader and more open-ended than they are in most laboratory studies of learning.

Are Primates Special?

Across the animal kingdom, brain size increases with body size. Despite this common scaling principle, however, brain size-to-body-weight ratios differ from one taxonomic group to another. Among mammals, primates have brains that are, on average, larger than the brains of similar-sized nonprimate mammals. They have a higher “index of cranial capacity” (ICC, Martin 1990).

The social intelligence hypothesis (Jolly 1966; Humphrey 1976) attempts to explain this difference. It proposes that all group-living animals confront a multitude of social problems, but that the problems facing primates are more daunting than those facing other species because primate groups are larger, their social relationships more complex, and their frequent formation of coalitions requires a more sophisticated knowledge of other animals' relations (Harcourt 1988; Dunbar 2000). The data reviewed in this chapter demonstrate that primates have an impressive knowledge of their companions' social relationships. But are primate societies really more complex, and is their social intelligence really superior to that found in other species? The issue is currently unresolved.

Some comparative tests of captive apes, monkeys, pigeons, and other animals suggest that primates are more adept than nonprimates at classifying items according to their relative relations (for reviews see Tomasello & Call 1997; Cheney & Seyfarth 2007; Shettleworth 2010). However, there is also good evidence that social complexity and large brains have coevolved in nonprimate species as well as in monkeys and apes. Large group size is positively correlated with larger neocortex size not only in primates (Barton & Dunbar 1997), but also in carnivores (Barton & Dunbar 1997), toothed whales (Connor et al. 1998), and ungulates (Perez-Barberia & Gordon 2005).

Moreover, many nonprimate species display examples of social cognition that rival those found in monkeys and apes.

When competing over access to females, male dolphins (*Tursiops truncatus*) form dyadic and triadic alliances with specific other males, and allies with the greatest degree of partner fidelity are most successful in acquiring access to females (Connor 2007). Field observations suggest that opponents may recognize the bonds that exist among others and selectively retreat when they encounter rivals with a long history of cooperation. Like many primates, lions (Packer & Pusey 1982), horses (Feh 1999), spotted hyenas (Engh et al. 2005), and dolphins (Connor & Mann 2006) intervene selectively on behalf of the higher-ranking animal when forming a coalition (but see Jennings 2009 for the opposite result among deer). Of course, selective intervention could occur simply because individuals intervene on behalf of winners. Arguing against this view, however, hyenas sometimes redirect aggression toward other, previously uninvolved individuals after a fight. When this occurs, they are more likely to attack a relative of their former opponent (Engh et al. 2005). Hyenas also seem to make transitive inferences about other individuals' dominance ranks (Engh et al. 2005). As already noted, pinyon jays recognize other individuals' dominance ranks and use that information to make transitive inferences about the ranks of unfamiliar individuals (Bond et al. 2003; Paz y Miño et al. 2004). Striking examples of social cognition have even been found in monogamous birds (e.g., Peake et al. 2002) and fish (Oliveira et al. 1998; Grosenick et al. 2007), where individuals “eavesdrop” on competitive interactions and remember the identities of winners and losers. These data refute the conclusion that there is a simple causal relation between large group size and knowledge of other animals' relations.

To summarize, while nonhuman primates have a higher ICC than other vertebrates, we cannot yet conclude that this difference has evolved as a result of greater social complexity. Primate societies are complex, and primates' knowledge of each other's social relationships is increasingly well documented, but we cannot yet demonstrate that either their societies or their social knowledge is more complex than that of other species.

The Role of Social Cognition in Primate Evolution

The social intelligence hypothesis argues that perception and cognition in primates have been shaped by the demands of social life—in other words, that primates recognize other animals' relations because such knowledge is essential to their survival and reproduction. This argument rests on two assumptions: first, that the formation of social relationships has a positive effect on reproductive success; and second, that in order to form the most adaptive social bonds, individuals must know about other animals' relations. The

first assumption is now well supported; the second is more speculative.

As Silk demonstrates in chapter 24 of this volume, we now have good evidence from studies of baboons and rhesus macaques that the formation of close, enduring social relationships in females reduces stress (Beehner et al. 2005; Engh et al. 2006a, b; Crockford et al. 2008; Wittig et al. 2008; Brent et al. 2011), increases infant survival (Silk et al. 2003, 2009), and increases females' longevity (Silk et al. 2010b). Similar benefits have been documented in horses (Cameron et al. 2009) and dolphins (Frere et al. 2010). Among males, the formation of close, enduring social relationships increases reproductive success in chimpanzees (Nishida & Hosaka 1996; Constable et al. 2001; Boesch 2009), Assam macaques (*Macaca assamensis*, Shülke et al. 2010) and dolphins (Kopps et al. 2010). All of these data support the assumption that close social relationships lead to improved reproductive success.

With regard to social knowledge, it is now clear that individuals in many species observe other animals' interactions and use the information they acquire about others to adjust their own behavior (see Cheney 2011 for review). Is such voyeurism adaptive? We do not yet know, because thus far no study has documented individual differences in social knowledge and linked them to differences in survival or reproduction. At this point, we can only propose that individuals must know as much as possible about other animals' relations—that is, they must have a sophisticated understanding of the individuals in their group, their long-term associations, their short-term bonds, and the motivations that underlie them—if they are to form the social relationships that return the greatest benefit. Social cognition, we suggest, is therefore essential to survival and reproduction (Cheney & Seyfarth 2007).

Summary and Conclusions

Primates live in groups characterized by differentiated social relationships: animals do not interact at random (chapter 23, this volume). Their social environment is thus characterized by predictable patterns of interaction—statistical regularities that an individual must recognize if she is to predict other animals' behavior. Studies of social knowledge demonstrate that individuals do recognize the relationships that exist among others. They recognize other animals' dominance ranks and the close, enduring bonds formed among kin. They also combine their knowledge of kinship and rank, grouping animals simultaneously along two dimensions. Field experiments indicate that baboons recognize when a vocalization is directed at them, thus

suggesting that they attribute motives to others. Further, when baboons hear an aggressive vocalization from one individual and a submissive vocalization from another, they respond as if they assume that one call has caused the other. Their social knowledge thus includes some recognition of causality.

It remains unclear whether primates' social knowledge can be explained as simply the “scaling up” of simple conditioning mechanisms like those found in laboratory studies. Nor do we know whether primate social knowledge is qualitatively different from that found in other species; although nonhuman primates have a higher index of cranial capacity than other vertebrates, we cannot yet conclude that this difference has evolved as a result of greater social complexity. Finally, there is at present no clear, explicit link between social knowledge and reproductive success. We can only propose that individuals must know as much as possible about other individuals' relations if they are to form the social relationships that return the greatest benefit.

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